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The Flexibility of Chemosensory Preferences

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INTRODUCTION

Immutability Versus Flexibility of Chemosensory Preferences

The title of this chapter – "The flexibility of chemosensory preferences" is constructed of three key terms that we need to define before moving forward: chemosensory, preferences and flexibility. Chemosensory preferences refer to preferences regarding odors, flavors and tastes (a definition of these terms is provided in the glossary at the end of the chapter). There are numerous definitions of the term preferences in the literature. Here, we will consider a preference towards X (X being a smell or a flavor) as an "indicator of the subjective expected value of engaging in goal-directed behavior towards object X" (Changizi & Shimojo, 2008). This definition includes both a component of valuation (liking X more than Y) and a behavioral tendency (in particular, approaching/withdrawing and choosing/rejecting). Finally, flexibility underlines the focus of this chapter on the changeable character of chemosensory preferences.

The central topic of this chapter will be how and to what extent chemosensory preferences can be modulated. However, before tackling this question, we will consider evidence that adopts the opposite perspective, i.e., in what way chemosensory preferences can be argued to be, at least partially, innate and hard wired (Steiner, 1979), and as such, rather inflexible. To do so, we will briefly review two main lines of evidence supporting this idea.

First, newborns display characteristic facial patterns as a function of hedonic variations of odors and tastes (Steiner, 1974, 1979). For example, in three-day-old infants, butyric acid, which is a rather unpleasant smell, elicits significantly more facial markers of disgust than vanillin, which is on average considered a pleasant smell (Soussignan, Schaal, Marlier & Jiang, 1997). These facial patterns are strongly homologous to those of other primate species, especially the species that are phylogenetically our closest relatives (Steiner, Glaser, Hawilo & Berridge, 2001). Chemosensory preferences could be shared across species and be partially genetically determined. For example, the lifelong taste preference for sweetness might have a genetically coded component (Keskitalo, Knaapila, Kallela et al., 2007). This suggests a genetically based and predetermined component of olfactory and gustatory preferences (see also the work of Mandairon, Poncelet, Bensafi & Didier, 2009, on olfactory preferences shared across mice and humans).

Second, some physicochemical properties of odorant molecules can predict how humans will perceive their hedonic character (Khan, Luk, Flinker et al., 2007). Moreover, such properties can allow an artificial nose to categorize the odors according to their pleasantness with high accuracy (Haddad, Medhanie, Roth et al., 2010). These results suggest that there is a predictable link between odorant structures and stimulus pleasantness.

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Chemosensory preferences develop very early, as early as when a child is still in the womb, influenced by the mother's diet (Beauchamp & Mennella, 2009; Schaal, Marlier & Soussignan, 2000; Schaal, Soussignan & Marlier, 2002). Thus, early and regular exposure at the mother's breast to a given smell has an impact on a child's preference for the smell itself. There is also evidence that such exposure has an impact on a child's behavior at 7 and 21 months of age toward objects with the same smell (Delaunay-El Allam, Soussignan, Patris et al., 2010). Moreover, early exposure to a smell (Poncelet, Rinck, Bourgeat et al., 2010), such as first associations between an odor and an object, may have a "privileged brain representation," in particular in terms of hippocampus activity (see Yeshurun, Lapid, Dudai & Sobel, 2009).

Despite this evidence, some authors have insisted that the olfactory system allows flexibility in dealing with the environment and high plasticity in responsiveness to odors (e.g., Engen, 1979, 1988). A significant body of evidence substantiates the claim of flexibility. For instance, cultural background and experience have been shown to matter more than genetics for preferences regarding sweet tastes (Mennella, Pepino & Reed, 2005). An appreciation of bitter tastes can be acquired across life, despite a newborn's reaction of disgust to these tastes (Mennella et al., 2005). The extent to which chemosensory preferences are flexible has been increasingly investigated not only at the behavioral level, but also at the cerebral level. Our perspective on the corpus of data on this research topic will be presented in greater detail below.

Aims and Structure of this Chapter

Here, we will review empirical results regarding the flexibility of chemosensory preferences, focusing on two aspects: (1) the nature of the influences that could modulate chemosensory preferences, and their neural underpinnings, as far as they are understood today; and (2) the generality of the mechanisms underlying the flexibility of chemosensory preferences, i.e., the degree to which the same mechanisms extend to other types of sensory preferences.

To do so, we will present the key factors that modulate chemosensory preferences. The valuation of any sensory stimulus depends on a number of factors, some of them shared across sensory modalities, others more tightly linked to specific sensory systems. We will restrict our attention to the factors that are most strongly linked with chemosensory processing. In particular, we will discuss modulatory factors as they relate to the three basic functions of the chemosensory system. These functions can be classified into three main categories: ingestion (e.g., appetite regulation); avoidance of environmental hazards (e.g., detection of

microbial threats); and social communication (e.g., emotional contagion) (Stevenson, 2010).

This chapter is structured as follows. First, we briefly present how needs, goals and values relate to chemosensory preferences. Second, we emphasize the role of learning and exposure in the flexibility of chemosensory preferences. Third, we discuss the importance of other sensory (e.g., visual inputs), decision-making (i.e., choices) and cognitive (e.g., verbal labels) information in the flexibility of chemosensory preferences. Pertinent data on the neural underpinnings of the described phenomena are presented throughout the chapter, where applicable.

NEEDS, GOALS AND VALUES IN THE FLEXIBILITY OF CHEMOSENSORY PREFERENCES

As mentioned earlier, the chemosensory system is intimately linked to ingestion, avoidance of environmental hazards and social communication. As such, it provides the organism with assistance for answering questions such as: "Shall I eat the rest of this dish that has been sitting in my fridge for two days, or should I cook something new?" "Shall I approach or stay away from this person?" "What self-image do I want to communicate by wearing a perfume during this romantic dinner?"

The aim of the following part of this chapter is to provide insight into how needs, goals and values are able to modify preferences regarding smells and flavors. The role of the amygdala and the orbitofrontal cortex (OBC) in such modulation is also presented.

Impact of Needs, Goals and Values on Chemosensory Preferences

Needs and Chemosensory Preferences

Needs refer to a psychological entity assumed to arouse actions towards goals that a person would pursue for their satisfaction (Gendolla, 2009). For instance, the need for nourishment is intimately connected with the goal of food intake. Preferences regarding such a goal depend notably on both the quality and quantity of previously ingested food. Regarding the quantity of already ingested food, one study showed that even if chocolate was rated as pleasant at the beginning of an experiment, the more chocolate that participants consumed, the less the chocolate was rated as pleasant (Small, Zatorre, Dagher et al., 2001).

There is evidence that such preferences related to food intake may be coded by the activity of the OBC cortex. Its activity is related to the representation of the affective value of smells (Rolls, Grabenhorst & Parris, 2010; Small, Bender, Veldhuizen et al., 2007) and tastes (Rolls, Critchley,

Verhagen & Kadoshisa, 2010) and more generally to the affective value of stimuli, independently from their sensory modalities. Even more generally, there is evidence that OBC activity is related to social and monetary stimuli (Grabenhorst & Rolls, 2011; Rolls & Grabenhorst, 2008). Crucially for our point here, appetite modulates OBC cortex activity, the activity of which is decreased after consumption to satiety of chocolate (Small et al., 2001), bananas (O'Doherty, Rolls, Francis et al., 2000), tomato juice or chocolate milk (Kringelbach, O'Doherty, Rolls & Andrews, 2003). Regarding the quality of already ingested food, a phenomenon called sensory-specific satiety elicits modulation of food pleasantness. Thus, the decrease in pleasantness of the sensory properties of a food eaten to satiety (Rolls, Rolls, Rowe & Sweeney, 1981) is larger than the corresponding decrease for foods that have not been eaten. This phenomenon also applies to foods that share sensory properties of the eaten food (Rolls, Vanduijvenvoorde & Rolls, 1984).

Thus, the pleasantness of food items can be modulated by how much and which type of food has already been ingested. As appetite and food intake are by definition in constant change, preferences regarding food items appear to have a highly modulated character.

Goals and Chemosensory Preferences

Goals are another important factor for food intake preferences. You might, for example, eat tofu rather than meat if your current goal is to keep your vegetarian co-workers happy, even if you like meat more than tofu. The impact of diet on food consumption preferences has been experimentally studied, both at the behavioral and at the neural level. Results have shown that participants trying to control themselves chose unhealthy but tasty food items less frequently than did participants who were not trying to control themselves (Hare, Camerer & Rangel, 2009). Moreover, in a food consumption context, the decisions of dieters, as well as non-dieters, were related to the activity of the ventromedial prefrontal cortex; this activity correlated with the expected reward that was associated with the consumption of a given food. But in contrast to the decisions of non-dieters, dieters' decisions were also related to dorsolateral prefrontal cortex activity, which plays a role in self-control (Hare et al., 2009). The pursuit of a goal such as losing weight consequently modified food consumption preferences in dieters.

This impact of goals on chemosensory preferences is far from being an exception. Goals have been shown to impact preferences in many domains (see Warren, McGraw & Van Boven, 2011, for a review).

Values and Chemosensory Preferences

Values are defined as broad motivational constructs that determine what we consider important and which goals we choose to pursue (Rohan, 2000). For instance, the value of self-interest has been shown to impact the amount of money given during a charitable task, as well as the activity of the reward system while engaging in this activity (Brosch, Coppin, Scherer et al., 2011). But does the influence of values also extend to the domain of chemosensory preferences? The answer is yes: when there is a match between one's most important values and the value symbolized by a product, the product tastes better (Allen, Gupta & Monnier, 2008). To give a concrete example, we first need to point out that the consumption of red meat is correlated with the value of social power, while vegetables and fruits symbolize the rejection of social power (Allen & Ng, 2003). This correlation has been shown in three studies that measured human values together with attitudes towards different types of foods by means of questionnaires (Allen & Ng, 2003). Experimental evidence showed that participants who reject social power evaluated a vegetarian alternative to a sausage roll as more tasty and had a higher purchase intention. This effect was independent of the food they actually tried (Allen et al., 2008).

Here again, the impact of values on chemosensory preference is similar to results reported in other areas of research regarding preferences. For example, values have been shown to at least partially influence preferences for a relationship partner (Goodwin & Tinker, 2002).

Amygdala: A Central Structure in Needs-, Goals- and Values-Related Relevance

According to Gottfried (2010), "the function of sensory systems is optimized to detect and encode behaviorally relevant events (objects) that are encountered in the real world" (p. 637). Needs, goals and values all contribute to the relevance of a given chemosensory stimulus. In other words, a smell or a flavor can have a different significance across different individuals and different contexts, depending on current needs, goals and values. This differential importance of a smell or a flavor across individuals and contexts may lead to changeable preferences towards it, as discussed earlier.

In terms of neural underpinnings, the amygdala is known to be activated by odors (de Araujo, Rolls, Velazco et al., 2005; Gottfried, 2008). The amygdala has also been proposed to act as a "relevance detector" (Coppin & Sander, in press; Pessoa, 2010; Sander, Grafman & Zalla, 2003; Sander, 2009; Sander, in press). In the olfactory domain, highly aversive olfactory (Zald & Pardo, 1997) and gustatory (Zald, Lee, Fluegel & Pardo, 1998) stimulation can be considered very relevant – and has been shown to elicit amygdala activity. However, amygdala activity is not just related to aversive chemosensory stimulations. Winston, Gottfried, Kilner and Dolan (2005) have shown that the amygdala responds to a combination of valence and intensity, which could reflect the overall relevance of a given smell. In the gustatory domain, Small, Velduizen, Felsted et al.

(2008) suggested that the amygdala, together with the thalamus, may predict the meaningfulness or biological relevance of tastes and flavors.

What experimental evidence exists for this hypothesis? Amygdala activity was higher when participants were hungry compared with when they were not hungry during the visual presentation of food items (LaBar, Gitelman, Parrish et al., 2001). A similar pattern was found when participants were told to imagine being in a restaurant and choosing their favorite food from the menu (Hinton, Parkinson, Holland et al., 2004). The activation of the amygdala was also more pronounced when participants were reading food names that they particularly liked, compared with reading names of more neutral food (Arana, Parkinson, Hinton et al., 2003). By recording single neuron activity from the amygdala while participants were making purchase decisions about food items, Jenison, Rangel, Oya et al. (2011) showed that the amygdala response was linearly related to the value assigned to a given food. This representation seems to flexibly depend on the level of hunger of the participants. Both the amygdala and the OBC cortex responses to a predictive cue of the presentation of food-related smells were shown to decrease as a function of satiety (Gottfried, O'Doherty & Dolan, 2003).

Taken together, the findings suggest that amygdala activity is related to the importance of smells and flavors in a given context, and more generally, to the relevance of a stimulus or a situation (Sander et al., 2003). Note that relevance is highly flexible across time and space and can be acquired and modified. This may explain why some authors such as Köster (2002) think that it is absurd to ask people the question "Why do you like this food?" Why we like smelling or eating something at a particular point can depend on numerous and variable factors that we are not necessarily aware of.

In the next part of this chapter, we will discuss the role of learning and exposure in modulating, and even creating, preferences for smells and flavors.

THE ROLE OF LEARNING AND EXPOSURE FACTORS IN THE FLEXIBILITY OF CHEMOSENSORY PREFERENCES

The Role of Aversive and Appetitive Conditioning

Olfactory learning is crucial for allowing flexibility and adaptation in a given olfactory environment (Hudson & Distel, 2002). One way to achieve learning is by means of conditioning, which has been extensively studied in the context of preference creation and modulation (e.g., De Houwer, Thomas & Baeyens, 2001). Conditioning can allow the discrimination, both perceptually and cortically, of previously

non-discriminable odor enantiomers, which are mirror-image molecules (Li, Howard, Parrish & Gottfried, 2008).

Aversive and appetitive conditioning also plays an important role in preference learning and modulation, both for olfactory and gustatory stimuli. Regarding aversive conditioning, the smell of eugenol, for example, is rated as unpleasant by participants who fear going to the dentist, probably by association with potentially painful dental treatment (e.g., Robin, Alaoui-Ismaïli, Dittmar & Vernet-Maury, 1999). In the gustatory domain, the power of aversive conditioning is even more impressive: a conditioned taste aversion requires only single-trial learning and works despite a long delay between a given taste and an illness (Bernstein, 1991; Garcia, Hankins & Rusiniak, 1974). Regarding appetitive conditioning, food preference reinforcement can have two sources: so-called flavor-flavor learning and flavor-nutrient learning (Ackroff, 2008). Flavorflavor learning consists of the increased evaluation of flavors by association with already preferred flavors (such as a sweet flavor; e.g., Fanselow & Birk, 1982). Flavor-nutrient learning represents the increased hedonic character of flavors whose ingestion is followed by the pleasant effects of the nutrients. The cerebral structures underlying this second type of preference learning have recently been investigated in humans. The cerebral areas involved are the striatum, the amygdala and the medial OBC cortex (Fobbs, Veldhuizen, Douglas et al., 2011).

Learning includes – but is not restricted to – aversive and appetitive conditioning. The mere repetitive exposure of a smell or a flavor can be another important type of learning, as it leads to the creation or the modulation of its hedonic evaluations.

The Role of Exposure

The Creation of Chemosensory Perception

Androstenone is a particularly interesting molecule for investigating the creation of olfactory perception and preference. A large part of the population cannot smell this odorant (approximately 40% of individuals cannot perceive an odor when presented with androstenone; Boyle, Lundström, Knecht et al., 2006). When not perceived, "smelling" androstenone is rated as neither unpleasant nor pleasant. It is, however, possible to acquire the capacity to perceive androstenone after repeated exposure (e.g., Wysocki, Dorries & Beauchamp, 1989). Once this ability has developed, androstenone is on average perceived as unpleasant.

The Mere Exposure Effect with Olfactory Stimuli

The mere exposure effect (Zajonc, 1968) has been reported to affect preferences in a variety of settings. Its effect on smells is of particular interest, because the effect of repeated exposure to smells may be

somewhat complementary to the survival relevance of quick and powerful taste aversions (Delplanque, Grandjean, Chrea et al., 2008).

As in other sensory domains, a high correlation between familiarity and pleasantness has been reported in the olfactory domain (e.g., Cain & Johnson, 1978). If this is a causal relationship, then repeated exposure to a smell increases one's preference towards it. However, this relationship would not be true for all types of smells: an increased preference occurs only for initially neutral to positively evaluated odors, but not for negatively evaluated odors (Delplanque et al., 2008). This non-extension of the mere exposure effect to negative odors may be understood regarding the high relevance of malodors for survival. Given the importance of olfaction for ingestion behaviors (Stevenson, 2010), it would not be adaptive to start liking, and possibly to have an appetite for or to approach, something that is potentially lethal just because of repeated exposures.

This selectiveness of the mere exposure effect has also been demonstrated in the case of interpersonal evaluations, depending on the reward versus punishment associated with seeing a particular person. The more a given person was seen, the more the person was liked, but only when he or she was associated with the delivery of a reward and not when associated with a punishment (Swap, 1977).

The Role of Culture and Social Appraisal

The frequency of exposure to different kinds of smells and foods is highly dependent on one's culture. Although common folk psychology suggests that "there is no accounting for taste," it is in practice not uncommon for people to criticize one another's culinary tastes when these are perceived as bizarre – particularly across cultural divides. For example, anecdotally, the British humorously call the French "frogs" – because frog's legs are considered a delicacy in France, but not typically in Britain. Similarly, baby mouse wine (a bottle of rice wine containing the bodies of baby mice) may not sound as appealing to foreigners as it does to its consumers in China and Korea, where it is available.

In scientific research, culture has been demonstrated to be a powerful force in olfactory (Ayabe-Kanamura, Schicker, Laska et al., 1998; Ferdenzi, Schirmer, Roberts et al., in press; Moncrieff, 1966) and gustatory (Bourdieu, 1984; Wright, Nancarrow & Kwok, 2001) preferences. The smell of durian, a common fruit in Asia with a very powerful and characteristic aroma, evoked feelings of disgust in Geneva or Liverpool, while it was evaluated as mainly pleasant in Singapore (Ferdenzi et al., in press). Directly related to culture, identity might also be an important factor in the perception of identity-relevant smells. Thus, the olfactory perception of chocolate, for which Switzerland is world famous, is modulated by accessibility to the Swiss identity in Swiss participants (Coppin, Delplanque, Cayeux et al., 2011a).

The concept of social appraisal probably also plays a particularly important role here. Social appraisal (Manstead & Fischer, 2001) globally refers to social influence on the appraisal of a given stimulus or person. It has been shown to notably influence women's preferences for men. Thus, a man being looked at by a smiling woman is going to be perceived as more attractive than is a man being looked at by a woman with a neutral facial expression (Jones, DeBruine, Little et al., 2007). Similarly, in the chemosensory domain, seeing another person eating meat with a neutral or happy facial expression versus a disgusted facial expression affects the desire to eat such food (Rousset, Schlich, Chatonnier et al., 2008).

More generally, social context can impact food preferences. For example, the desire to eat decreased when an obese person was observed, independently of his or her facial expression. In contrast, the desire to eat increased when a person of normal weight was seen with a facial expression of pleasure (Barthomeuf, Rousset & Droit-Volet, 2010). This effect was not observed in children (Barthomeuf, Droit-Volet & Rousset, 2011). In children, the desire to eat seems to be more influenced by the eater's emotional facial expression than by his or her weight. Such results suggest flexibility in the relevance of social context factors for food preferences, as well as flexibility in food preferences.

The extent to which social factors modulate preferences generally is discussed by Campbell-Meilkejohn and Frith (Chapter 8 of this book).

In summary, learning, such as through conditioning or mere exposure, if broadly embedded in a given social context and culture, constitutes a very powerful way to modulate preferences for smells and flavors. The intrinsic emergence of chemosensory perception in an information-rich environment invites further consideration of the role of other sensory inputs and/or cognitive information in smell and food preferences. This is the topic of the following section of this chapter.

THE ROLE OF OTHER SENSORY INPUTS AND COGNITIVE FACTORS IN THE FLEXIBILITY OF CHEMOSENSORY PREFERENCES

Information from Other Sensory Modalities and Decision-Making Influences

Impact of Inputs from Other Sensory Modalities

Chemosensory perception occurs in a world full of simultaneous visual, auditory and tactile sensory inputs, which influence it. Olfactory detection is more rapid and more accurate when smells are presented with congruent visual cues (e.g., Gottfried & Dolan, 2003). In addition to mere perception, the interaction between the different sensory systems, such

as the perceived match between a color and a smell, alters chemosensory pleasantness. For example, the smell of strawberry-flavored drinks is more pleasant when the drink is red than when it is green. The activity of caudal regions of the OBC, as well as those of the insular cortex, increases with the perceived congruency between a given color and an odor (Österbauer, Matthews, Jenkinson et al., 2005). Smells can also be associated with some abstract, visually presented symbols, and the congruency between a given smell and a given symbol can modify its pleasantness (Seo, Arshamian, Schemmer et al., 2010). In addition to visual information, the presentation of smells and foods is often associated with sounds. Auditory information may also play a role in the perception of olfactory pleasantness. A smell is perceived as being more pleasant when evaluated while listening to a congruent sound rather than an incongruent sound. Moreover, hearing a pleasant sound right before the presentation of a smell will increase the smell's perceived pleasantness (Seo & Hummel, 2011).

Impact of Decision-Making Processes

In the plethora of information available, that related to decision-making is particularly relevant for the discussion of the flexibility of preferences. The influence of choice on subsequent preferences (Brehm, 1956) is discussed in other chapters of this book (Johansson, Hall & Chater, Chapter 6; Sharot, Chapter 3) and will consequently not be developed here. It is, however, worth noting that post-choice preference modulation has also been reported for smells (Coppin, Delplanque, Cayeux et al., 2010) and tastes (Hall, Johansson, Tärning et al., 2010). After a choice between two similarly liked smells or tastes, the chosen one is rated as "more pleasant," and the rejected one as "less pleasant," in comparison to the ratings made before the choice. This modulation of olfactory preferences by choice may be implicit (Coppin et al., 2010) and remains stable even a week later (Coppin, Delplanque, Cayeux et al., 2011b).

Verbal Labeling and Expectations

Verbal Labels and Smells

The impact of verbal labels on olfactory-perceived pleasantness has been shown to be quite dramatic: the same odor is perceived as more pleasant when presented with a positive rather than a negative verbal label (Djordjevic, Lundstrom, Clément et al., 2008; Herz & von Clef, 2001; Herz, 2003). For example, when presented without a label, isovaleric acid is typically evaluated as highly unpleasant. Labeling this smell as "cheddar cheese" leads to more pleasant evaluations than does labeling it as "body odor" (de Araujo et al., 2005). Moreover, correlated with these pleasantness ratings, the rostral anterior cingulate cortex (ACC) and the

medial OBC were more activated during the "cheddar cheese" label than during the "body odor" label, although the odor was identical (de Araujo et al., 2005). The activation of the ACC can be related to its supposed role in coding the subjective pleasantness of many types of stimuli and to link such a representation to goal-directed actions. These results suggest that the medial OBC may respond to pleasant smells, even when pleasantness is modulated by cognitive information. Grabenhorst, Rolls and Bilderbeck (2008) similarly found that a flavor labeled "boiled vegetables water" led to less pleasant evaluations than the same flavor labeled "rich and delicious flavor." The labels modulated the activity of the OBC, as well as the pregenual cingulate cortex, in response to flavors.

Expectations and Flavors

Expectations can be driven by many factors, but a very common one in everyday choices is price. Studies in this area have notably been conducted using wines. Wine is an interesting beverage because it is considered much more than simply a source of nutrition, being more related to culture, values and social status (Colman, 2008). While pleasantness between different wines was not significantly different when they were presented with no price information, pleasantness was correlated with price when the wines were presented with made-up prices. When the wines were presented with prices, pleasantness ratings were correlated with medial OBC activity (Plassman, O'Doherty, Shiv & Rangel, 2008). Expectations may therefore modulate the hedonic value of a wine via the activity of the OBC, whose role in hedonic representation was discussed earlier. Interestingly, during blind tastings, the correlation between price and the overall rating of a wine was small and negative. Such a result means that, on average, people enjoyed drinking the more expensive wine used in the study slightly less, when they did not know its price (Goldstein, Almenberg, Dreber et al., 2008).

Similarly, receiving positive or negative information from wine experts about a wine that is about to be tasted also influences its hedonic evaluation and the willingness to pay for a bottle of this wine (Siegrist & Cousin, 2009). It is important to point out that expectations seem to modulate preference by influencing the *tasting experience itself* (see Lee, Frederick & Ariely, 2006). This conclusion is drawn from the observation that hedonic evaluation and willingness to pay for a bottle of wine are not affected if the wine expert's information is given *after* the tasting.

The Influence of Brands on Beverage Preferences

The role played by brands has been an important topic in understanding the dynamics of chemosensory preferences. Nevid (1981) used

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carbonated water beverages of two different statuses to investigate how an advertisement could lead to a particular preference. He used a high-status (Perrier brand) and a low-status (Old Fashioned brand) beverage. His results suggest that the quality was evaluated as being better when the beverage was Perrier in comparison to Old Fashioned. Such a preference towards Perrier was not found when the brands were not presented.

More recently, McClure, Li, Tomlin et al. (2004) have focused on two very famous soda brands - Coke and Pepsi - and demonstrated their impact on chemosensory preferences. These two drinks are almost the same in terms of their chemical composition, but most people display a strong preference for one rather than the other. Behaviorally, results were very similar to what Nevid found with carbonated water beverages: when the two beverages were tasted with no information about the brand in a double-blind taste test, participants' preferences were split equally. In terms of neural underpinnings, two different systems seemed to be involved in preferences. When no brand information was available, the activity of the ventromedial prefrontal cortex was correlated with participants' preferences for the drinks. However, when brand information was available, the dorsolateral prefrontal cortex, hippocampus and midbrain also showed activation that correlated with participants' preferences for the drinks. These results raise the possibility that hedonic perception is modulated by prior affective experience. Consistent results have been obtained for car brands, where culturally familiar car logos have been shown to activate the medial prefrontal cortex (Schaefer, Berens, Heinze & Rotte, 2006). Thus, brands may lead to strong preferences towards one item rather than another, despite the absence of important differences in the product attributes.

CONCLUSION

In terms of neural underpinnings, several cerebral areas are known as generally important in chemosensory processing, such as the amygdala, the piriform cortex or the rostral entorhinal cortex (see Gottfried, 2010, for a review). Regarding the flexibility of chemosensory preferences more specifically, two cerebral regions seem to be particularly involved: the amygdala and the OBC cortex. The amygdala appears to act as a relevance detector (Sander et al., 2003) for stimuli that are particularly important in a given context, notably smells and flavors. The evidence further suggests that OBC cortex activity encodes the current hedonic value of a smell. Other structures such as the ACC also appear to be involved in the coding of olfactory and gustatory preferences, notably in directing goal-directed actions, such as approach or withdrawal.

The extent to which chemosensory preferences are fixed is highly debated in the literature. While some authors have argued that chemosensory pleasantness perception is to some extent predetermined (e.g., Khan et al., 2007), other authors have insisted that the intrinsic ambiguity of olfactory perception makes it more likely to be modulated by non-olfactory factors (e.g., Gottfried, 2008). According to the latter view, chemosensory preferences are related to physicochemical properties, but can be strongly modulated by factors such as those addressed in this chapter, in particular learning, exposure, needs, goals and values.

Glossary

- **Flavor** Flavor perception is the result of the combination of different sensorial inputs: tastes, smells and oral somatosensory sensations (McBurney, 1986; Small, 2008b) and possibly of visual and auditory cues (Auvray & Spence, 2008).
- Odor Odors have been defined as the "perceived smells that emanate from an odorant or mixture of odorants," an odorant being "a chemical stimulus that is capable of evoking a smell" (Gottfried, 2010). As such, odors refer to subjective constructs and can consequently be modulated by many influences (Hudson & Distel, 2002).
- **Taste** The term "taste" can be considered as a more commonly used word to refer to the concept of "flavor" (Small, 2008a).

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